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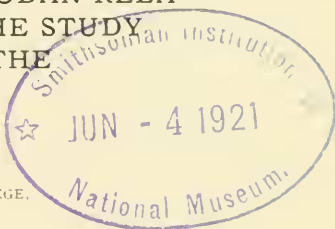
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THE PHYLOGENETIC ORIGIN OF THE MANDIBLES
OF INSECTS AND THEIR ARTHROPODAN RELATIVES—A CONTRIBUTION TO THE STUDY
OF THE EVOLUTION OF THE ARTHROPODA.

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The study of the mandibles alone has furnished but a small portion of the evidence upon which the conclusions concerning the evolution of insects and their arthropodan relatives, set forth in the following series of papers, are based. It is obviously impracticable, however, to attempt to present all of the evidence available on the subject, in a single paper, since it would require too great a number of plates to illustrate the various features of comparative anatomy, embryology, etc., which must be considered in such a discussion. On this account, it has seemed preferable to present the evidence gained from a study of the remaining features of the comparative morphology of the mandibles (the origin of only one type in insects has been discussed in the present paper), as well as that gained from the study of the head capsule with its appendages, the trunk segments and their appendages, the terminal abdominal structures, the embryological development of the arthropods in question, and all other features having a bearing on the study of the phylogeny of the Arthropoda, in a series of papers dealing with each phase of the

subject separately; and the following discussion is therefore offered as the first of such a series of papers dealing with the more important features of value in the study of arthropodan evolution.

It is extremely difficult for anyone who is not a specialist in the Crustacea to obtain specimens of the rarer forms for dissection, and on this account, it has been necessary for me to depend upon the descriptions of others for the morphological details of certain of the rarer Crustacea such as the Euphausiacea, *Anaspides*, etc., but I have been fortunate in being able to examine representatives of these forms, and I have been able to dissect other types sufficiently close to these to enable me to form an opinion as to their relationships—and luckily, those types of Crustacea which are of the greatest importance for a study of the phylogeny of insects, are obtainable from the biological laboratories of Europe.

I would use this opportunity of expressing my very sincere gratitude to Miss Rathbun for the loan of a specimen of *Anaspides* and other interesting material from the U. S. National Museum, and to Dr. Calman of the British Museum for specimens of the interesting crustacean *Apscudes*. Dr. Chamberlin of the Harvard Museum has furnished me with interesting and valuable myriopodan material, and Dr. Walcott of the Smithsonian Institution has very generously given me a number of photographs of trilobitan appendages, and has very kindly allowed me to copy Fig. 18 (Plate VII) from his restoration of the appendages of the trilobite *Ncolenus*. I am also deeply indebted to Dr. Raymond of the Harvard Museum for much valuable information concerning the affinities of trilobites; and Fig. 9 (Plate VI) is based upon a restoration of the trilobite *Triarthrus* made by him.

GENERAL CONSIDERATIONS.

It is indeed astonishing that so little attention has been given to the evolution of the members of the phylum Arthropoda, since no other group of living things can equal or even approach them in the number of their species, in the multiplicity of their modifications of structure and habit, or in their preservation of synthetic types serving to connect the various subdivisions of the group. The survival of ancient types but little modified from their primitive condition, such for example as *Apus*, which has changed but little since Cam-

brian times, enables us readily to compare the more recently evolved forms with their "contemporaneous ancestors," and it is therefore frequently quite easy to obtain an almost unbroken series of stages illustrating the probable steps in the evolution of certain structures almost from the very inception of the development of the tendency on the part of these structures to assume their more modified aspects. Since I have been fortunate in obtaining an exceptionally fine series illustrating the probable course of the phylogenetic development of one type of insectan mandible, it has seemed preferable to make this the subject of the first paper dealing with the evolution of arthropods-related to insects.

Since no living types are strictly speaking "ancestral" to other living types (excepting in the case of mutants which have departed but little from the parent stock), it should be clearly understood that in employing a number of recent forms to illustrate the path of evolution followed in deriving the insectan type of mandible from the original arthropodan type of mandibular appendage, I would not imply that any one of the stages represented in the series is actually ancestral to the succeeding stages. On the other hand, certain primitive living forms have departed but little from the actual ancestors of other living forms in many respects, and those "ancestral" features which they have preserved in a very slightly modified form, serve to indicate the probable stages through which the parts of other more highly modified forms have passed, in assuming their present condition; and the study of such a series is of the greatest value in enabling us to gain a correct understanding of the nature of the parts in the higher forms.

As a rule, the student of trilobitan structures has confined his attention to this group alone, and the carcinologist is content to devote his energies to the study of the Crustacea alone, while those entomologists who have attempted to invade these fields have not been conspicuously successful in comparing the structures of insects with those of Crustacea and trilobites, with the result that the true nature of the parts of insects is not understood in many cases, and the most glaring misinterpretations of insectan structures have gained a dishearteningly widespread acceptance in the various textbooks and publications dealing with this phase of entomology. In this con-

nection I need but cite the universally accepted, though erroneous, conclusion that the "superlinguæ" of insects (which are the homologues of the paragnaths of Crustacea) represent the first maxillæ (maxillulæ) of Crustacea, and the resultant false conclusions that the first maxillæ of insects (which are homologous with the first maxillæ or maxillulæ of Crustacea) represent the second maxillæ of Crustacea, while the second maxillæ (labial appendages) of insects are incorrectly homologized with the first maxillipeds of Crustacea, instead of correctly homologizing them with the second maxillæ of Crustacea. As a consequence of these false views, the head of an insect is regarded by some entomologists as composed of seven segments (instead of but six, as embryology has long shown to be the case), and the true homologies of the structures of the head of an insect have been greatly confused.

Not only has the composition of the head in general been misinterpreted by many entomologists, but the nature of the parts of the mouth structures has not been properly understood, due to the fact that no one has apparently made a thoroughgoing comparison of these structures in insects, Crustacea and trilobites. Thus Chatin, Smith, and other entomologists who are apparently not aware of the fact that the mandible of an insect represents only *one* segment of a modified limb, while the "body" of the maxilla (not including the cardo and palpus) is composed of at least *two* segments of such a limb, have made the unfounded claim that the parts of the maxilla are repeated in the mandible; and such investigators as Hollis, 1872, or Heymons, 1896, who have mistaken the lacinia mobilis and processes of the incisor region of the mandibles of insects for so called mandibular "palpi," homologous with the mandibular palpi of Crustacea, are apparently not familiar either with the nature of the mandibular palpi of Crustacea, or with the structure of mandibles in various insects, since the structures occurring on the mandibles of insects which they attempt to homologize with the mandibular palpi of Crustacea, do not occur in the same position occupied by the palpi of the latter forms, and they have nothing of the nature of palpi to warrant interpreting them as such.

The fact that entomologists homologize the palpi of the maxillæ (or labium) with the exopodite of a crustacean limb, and homologize the galea and lacinia of the maxillæ with the endopodite of such a

biramous limb, clearly shows that they have not traced the modifications of the mouthpart limbs in a series of Crustacea leading up to the insectan type, in order to give an intelligent opinion in the matter; and the attempt of Wood-Mason, 1879, to homologize the incisor process of the mandible of *Machilis* with the exopodite of a crustacean limb, and to homologize the molar process of *Machilis*' mandible with the endopodite of a crustacean limb, well illustrates to what flights of fancy one may be led if he does not take the precaution of studying the modifications met with in the Crustacea and lower insects, before indulging in speculations concerning the interpretation of the structures of insects in terms of crustacean anatomy! Furthermore, the fact that an entomologist of the reputation of Folsom, 1900, should suggest that the mandibular palpi of Crustacea represent the exopodites of crustacean limbs, very clearly indicates (in addition to the other instances cited above) that entomologists in general are not sufficiently familiar with the developmental tendencies exhibited by Crustacea and other forms related to lower insects, to enable them to correctly analyze the conditions met with in lower insects. On this account, I have devoted the greater part of the present discussion to an attempt to trace the evolution of the mandibular appendage in those arthropods which approach the insectan type, instead of taking up the consideration of the evolution of the mandibles within the class Insecta—which I am hoping to discuss in a future publication on this subject.

ORIGIN OF ARTHROPODAN APPENDAGES.

The lines of descent of the Arthropoda are approached by those of the Onychophora, Tardigrada, Myzostomida and "Annelida"; but the lines of the descent of the Onychophora, Tardigrada and Myzostomida lead off toward paths of specialization which do not parallel that of the arthropods very closely, and the condition occurring in the appendages of these forms (see textfigures 9, 10, and 11) does not throw much light upon the subject of the nature of the precursors of arthropodan limbs, although a study of the condition found in the groups in question is not wholly without value. On the other hand, the annelids approach the arthropods in so many particulars, that I am more inclined to seek the type of structure foreshadowing an arthropodan

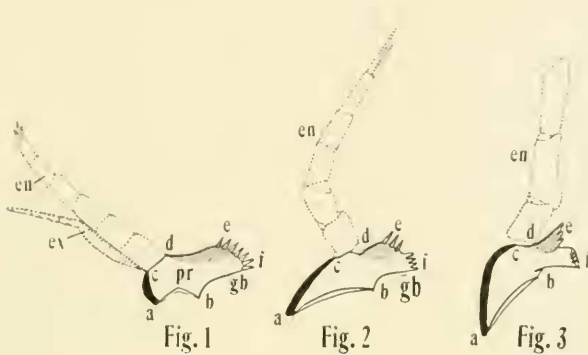
limb, in the so-called parapodia of the annelids (see textfigure 7) as is done by Borradaile, Boas, and many of the earlier zoölogists. It should be borne in mind, however, that in dealing with groups so far apart as the annelids and Crustacea, it is impossible to do more than guess as to what parts are homologous in the structures of the two groups, and the comparisons made below are more in the line of suggested possibilities, than definite statements of actual homologies.

In such annelids as *Laodice rubra* (textfigure 7) the anteriormost parapodium consists of a main axis "cn" which bears a ventral cirrus "ci" and a segmented dorsal cirrus "cx." The second parapodium likewise bears a dorsal gill "cp" (dotted in the figure, since it is not present in the first parapodium) attached near the base of the parapodium. In comparing the parts of such a parapodium with those of a typical crustacean limb (textfigure 8—compare also Fig. 21, Plate VII) the position of the gills "cp" of textfigure 7 corresponds in a general way to that of the gills or epipodites "cp" of textfigure 8, while the dorsal cirrus "cx" of textfigure 7 occupies a position somewhat suggestive of that of the exopodite "cx" of the crustacean limb (textfigure 8). The main axis of the parapodium labeled "cn" in textfigure 7 resembles the main axis of the crustacean limb ("cn" of textfigure 8) in position, while the ventral cirrus labeled "ci" in textfigure 7, is somewhat suggestive of the endite or "gnathobase" labeled "ei" in textfigure 8. It is also quite possible that the main axis of the crustacean limb labeled "cn" in textfigure 8, represents the main axis of the limbs "cn" shown in textfigures 9, 10, and 11. These in turn may correspond to the main axis "cn" of the parapodium shown in textfigure 7, although the main axis of the parapodium shows no signs of segmentation.

ORIGIN OF THE MANDIBLES.

Even such primitive worm-like forms as *Peripatus* have developed a mandible-like appendage in the mouth region (Fig. 31); but some investigators claim that the appendage in question in *Peripatus* is not strictly homologous with the mandibular appendage of Crustacea, insects and myriopods; and since the mouthparts of insects are merely modified limbs (as was pointed out over a century ago by Savigny, 1816, and has been confirmed innumerable times by embryological

investigations) we would expect that the most primitive type of mandible would be more like a walking-leg than a jaw-like appendage, and those arthropods in which the mandibular appendage is still in the "walking-leg stage" should therefore be taken as the starting



Textfigures 1 to 6 (compare with figures in plates) are diagrammatic representations of the stages in the development of the insectan type of mandible. For interpretation of lettering see list of abbreviations at end of paper. Textfigure 1. Mandibular limb of trilobite. Textfigure 2. Limb of merostome. Textfigure 3. Mandible of *Nebalia*.

point for tracing the evolution of the mandibular appendage in the higher forms.

Fortunately, in such primitive arthropods as the trilobites (*e.g.*, *Triarthrus becki*, which Beecher has studied with such signal success) we have an excellent starting point for the study of the evolution of the mouthparts of other arthropods, since in the trilobites the appendages which Beecher homologizes with the second antennæ, mandibles, first maxillæ, and second maxillæ of Crustacea, are all practically alike, and are almost exactly like the trilobite's "walking" legs. In fact, I know of no other arthropods which so well illustrate the fact that the mouthpart appendages are merely limbs of the "walking-leg" type adapted for holding and comminuting food. Since those mouthpart-limbs of a trilobite which are homologous with the second antennæ, mandibles, first maxillæ and second maxillæ of Crustacea, have not yet taken on the character of these appendages of the Crustacea, but are still "walking"-leg (or more accurately

"swimming" leg) like, I would refer to the appendages in question in the trilobite as protantennæ, protomandibles, protomaxillulæ and protomaxillæ, to indicate that they are the precursors of the second antennæ, mandibles, maxillulæ (first maxillæ) and maxillæ (second) of Crustacea, but have not yet become sufficiently modified to take on the form of these structures exhibited by the Crustacea, although the first antennæ (antennulæ) of trilobites have lost the walking-leg form and have taken on the character of true antennæ.

I have been astonished to find that in such ancient and apparently primitive Crustacea as *Apus* (Fig. 22) and *Branchippus* (Fig. 23) the mandibles have lost their original limb-like character and have assumed the form of true mandibular jaws. Even in the Copepoda (Fig. 30) and Ostracoda (Fig. 33) the mandibular appendages have become so far modified that the terminal portion of the mandibular limb has taken on the appearance of a palpus of the basal segment which forms the body of the mandible proper, despite the fact that the terminal portion of the mandibular limb (*i.e.*, the palpus) in these forms has still retained the inner branch "*en*" and outer branch "*ex*" of the primitive biramous crustacean and trilobitan limb (compare with textfigures 1 and 8, "*en*" and "*ex*"). On the other hand, the mandibular appendage (protomandible) of trilobites is almost exactly like a "walking" leg, and in the Merostomata, Pantopoda, Scorpionida, and the arachnoids in general, the appendage homologous with the mandibles of insects, myriopods, and Crustacea is more like a limb than it is like a jaw. I would therefore divide the arthropods into two subphyla, one of which the *Eugnathata* contains the Insecta, "Myriopoda," and Crustacea, and is characterized by the modification of the mandibular appendage to form a true mandible (with terminal segments either lost, or reduced to form a palpus); while the other subphylum, the *Podognathata*, contains the remainder of the arthropods, in which the mandibular appendage is essentially like a limb, the terminal segments being of such a character that they do not form a mere palpus-like organ for the basal jaw segment.

Such a division of the arthropods would group the trilobites with the Merostomata somewhat more closely than with the Crustacea, and such a grouping would be justified by the character of the head (which is flattened with the eyes located above), by the character of

the limbs (which have unjointed gnathobases in the two groups), and by the character of the segments and pygidium in trilobites and immature merostomes such as *Limulus*. On the other hand, the trilobites are very Crustacea-like in having biramous limbs, and other features strongly suggestive of crustacean affinities, and I would not minimize the fact that the trilobites are clearly annectant between the Crustacea and Merostomata; but, as I have pointed out in an article in the *American Naturalist*, and in the 51st Report of the Entomological Society of Ontario (Crampton, 1919A and 1919B) the main trend of the trilobitan developmental tendencies seems to lead more toward the development of the merostome type of arthropods, than toward the main line of the Crustacea and their descendants the myriopods and insects.

Raymond, 1920, who regards the trilobites as the ancestors of other arthropods, does not differ from me in this matter as fundamentally as his paper in the *American Naturalist* would imply, since I too regard the trilobites as very close to the ancestors of arthropods in general (as was stated in the article in the Report of the Entomological Society of Ontario for 1919); but I do not consider the trilobites as actual ancestors of the Crustacea such as *Apus*, etc. (and consequently of higher Crustacea also), since the Apodidæ were contemporaneous with certain trilobites, and the earlier trilobites combine in themselves so many apodid and crustacean features, that I cannot avoid the conclusion that the first arthropods were more of the nature of trilobitan-Crustacea (or crustacean-Trilobita) rather than pure trilobites; and the inherent tendencies which flowed into the purely trilobitan side of the early arthropodan lines of development are mostly those which lead to the merostome type, rather than to the types of development exhibited by the Crustacea, and their descendants the myriopods and insects.

To return to the subject of the origin of the mandibles of Crustacea and their allies, it would appear that the precursors of the mandibles were leg-like appendages of the biramous type (see text-figure 1, and Fig. 9 of Plate VI) in which the basal segment became modified for holding or comminuting the food, while the endopodite ("en" of textfigure 1, and Fig. 9) or inner branch of the limb, still served to aid in the locomotion of the creature, and the exopodite

("ex" of textfigure 1, and Fig. 9) of the limb doubtless served as a gill—or it may even have aided in locomotion as well. The probable paths of development followed in the evolution of the different types of mandibles of interest from the standpoint of the development of the insectan type, have been sketched below.

EVOLUTION OF THE MANDIBLES.

As was mentioned above, the trilobitan type of biramous mandibular appendage, in which the exopodite "ex" (textfigure 1) is still retained, and the endopodite "en" still functions in locomotion, while the basal segment (like that of the body limbs as well) has become modified in a fashion which enables it to function in the holding and comminuting of food, serves as a convenient starting point in tracing the series of modifications leading to the production of the insectan type of mandible. The mesal region of the basal segment of the limb is produced to form the so-called gnathobase "gb" (textfigure 1, and Fig. 9 of Plate VI) which abuts against its fellow projecting from the limb of the opposite side of the body, and serves to manipulate and comminute the food (which was probably of the nature of soft bodied worms or similar creatures, as is the case with *Limulus* and related forms living today). The gnathobase is provided with stout spine-like projections which doubtless aided in comminuting the food, and I think that a portion of the surface bearing these projections becomes involved in the composition of the incisor region of the mandibles of higher arthropods. It is possible that the endite "gb" of the basal segment of the limb of *Apus*, shown in Fig. 20 (Plate VII) corresponds to the gnathobase "gb" of the trilobite shown in Fig. 18 (or in textfigure 1); but the other endites "ci" of the limb of *Apus* (Figs. 20 and 19) appear to be articulated appendages of the limb differing slightly from the gnathobase "gb" which is a prolongation of the entire mesal region of the basal segment of the limb in the trilobite shown in Fig. 18, for example.

A somewhat higher stage of development is represented by the condition exhibited by a limb of the merostome *Limulus* shown in textfigure 2 (compare with Fig. 8, Plate VI). As may be seen in textfigure 2, there is a tendency to lose the exopodite ("ex" of textfigure 1) in the limb of a merostome, while the point of attach-

ment of the endopodite is thrown forward by the lengthening of the area from "a" to "c" in the merostome, as may be seen by comparing the extent of the area from "a" to "c" (marked with a black margin to make the comparison easier) in textfigures 1 and 2. In Fig. 14 (Plate VII) of the gnathobase of a limb of *Limulus*, the proximal spine-like projections are closer together, and stouter than the distal ones, and on this account, I have represented the spine-like projections in the area labeled "f" in the merostome shown in textfigure 2, as though they were becoming more massed together than is the case with the spines in the stippled area "e" of the gnathobase.

The chief differences between the stages shown in textfigures 1 and 2 are thus seen to be the loss of the exopodite "ex," the shifting forward of the endopodite "en" through the lengthening of the area from "a" to "c" (margined in black), the shortening of the area from "d" to "e" (i.e., the stippled area), and the differentiation of the "masticating" area into an upper area "e" and a lower area "f" in which the spine-like projections become more "massed together." While the merostomes do not stand in the direct line of descent of the Crustacea, but are on a side line leading to the arachnoid type of arthropod, the merostomes have nevertheless retained the condition of the limbs in a fairly primitive state, approaching the condition which was doubtless characteristic of the limbs of a number of primitive forms a little more modified than the trilobites; and on this account the condition exhibited by the merostome appendage may be taken as representative of the stage of development intermediate between the trilobite shown in textfigure 1 and the crustacean shown in textfigure 3, despite the fact that the character of the body as a whole, in the merostomes, exhibits more arachnoid than crustacean features.

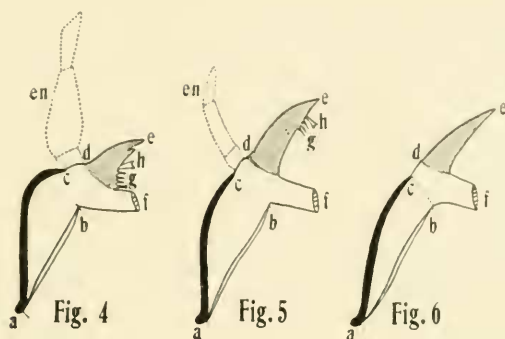
In the crustacean *Nebalia*, whose mandible is shown in textfigure 3, the mandibular appendage has taken on the character of a true mandible, through the reduction of the endopodite "en" to a three-segmented palpus, the differentiation of the "masticatory" area into a well defined incisor or biting area "e" (stippled in the figure), and a molar or grinding process "f," which is probably formed by the crowding together of the spine-like projections of the area labeled "f," and the elongation of this area to form the molar process "f"

of textfigure 3. The black margined area from "a" to "c" becomes proportionately longer, and arches over in such a fashion that the point of attachment from "a" to "b" instead of being more horizontal as in textfigures 2 and 1, tends to become more vertical (or obliquely so) in the mandibular appendage shown in textfigure 3.

If there were any question as to whether the palpus "cn" of textfigure 3 (compare also Fig. 10, Plate VII) represents the endopodite or the exopodite of a biramous limb, a glance at Fig. 33 (Plate VIII) will readily convince anyone that the exopodite "ex" becomes reduced and is eventually lost, while the endopodite is retained to form the palpus when the palpus is present. The mandibles shown in Figs. 30 and 33 (Plate VIII) would doubtless have furnished better intermediate stages than the merostome limb used in textfigure 2 to illustrate the transition from the type shown in textfigure 1 to that shown in textfigure 3, and these forms stand more nearly in the direct line of descent of the higher Crustacea; but there are certain features which the merostome limb illustrates better than these other forms, and the figure of a merostome limb serves well enough for the purpose intended.

Since there is only what appears to be a molar area "mo" in the mandible of the branchiopod *Branchippus* shown in Fig. 23 (Plate VIII), this suggests that the molar area "mo" of Fig. 23 may represent the entire "masticatory" area of the mandible of *Apus*, shown in Fig. 22. I am more inclined, however, to think that the region labeled "in" in Fig. 22 corresponds to the incisor area "in" of Fig. 10 (Plate VI) while the closely packed processes "mo" of Fig. 22 (Plate VIII) in the proximal portion of the masticatory area, may form the molar area "mo" of Figs. 10 and 23. In this connection, it should be noted that the mandible of *Apus* assumes the position shown in Fig. 24 when "in situ," and consequently it must be turned over and placed in an upright position as in Fig. 22, if it is to be compared with the mandibles of other forms, which have assumed the latter position. The fact that the molar process "mo" is the only portion of the masticatory area preserved in the shrimp shown in Fig. 26 (Plate VIII) makes it more readily comprehensible that the molar area might be the only portion of the masticatory area preserved in the branchiopod shown in Fig. 23; but I would not insist

upon the interpretation of the area labeled "mo" in Fig. 23, as the molar area alone, and I have only provisionally interpreted it as such until I have been able to study other related forms in order to definitely determine the point in question.



Textfigure 4. Mandible of *Mysis*. Textfigure 5. Mandible of *Apsudes*.
Textfigure 6. Mandible of *Machilis*.

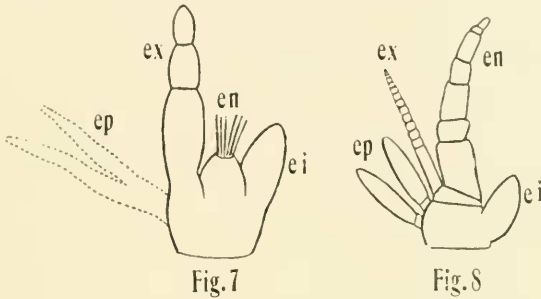
A stage beyond that represented in textfigure 3 is illustrated by *Mysis*, shown in textfigure 4 (compare also Fig. 7 of Plate VI). *Thysanopoda* or *Euphausia* would doubtless have proven to be much better in many respects than *Mysis* for such a phylogenetic study, but one must perforce do the best he can with such material as he is able to procure, and the Crustacea in question are among the number of certain interesting and much-needed specimens which I have as yet been unable to procure for study! *Mysis*, however, serves the purpose fairly well, and by comparing textfigure 4 of *Mysis*, with textfigure 3 of *Nebalia*, the following changes may be noted as we pass from the more primitive types of Crustacea to those which approach more closely to the types ancestral to the higher Crustacea, insects and "myriopods." The endopodite "en" (or mandibular palpus) becomes proportionately smaller as the basal segment of the mandibular appendage grows larger and becomes better adapted for chewing purposes. It is possible that the endopodite "en" of *Nebalia* (textfigure 3, or Fig. 10 of Plate VI) might be of some use in swimming. At any rate, it can beat outward with a movement which it would be apparently impossible for the endopodite "en"

of textfigure 4 (or Fig. 7) to execute, since the joints of the endopodite "cn" of *Mysis* (textfigure 4) are of such a nature that the endopodite is directed mesalward instead of outward as in *Nebalia* (textfigure 3).

The black margined area from "a" to "c" is of proportionately greater extent in textfigure 4 than in textfigure 3, and arches over more pronouncedly in the former (*Mysis*) than in the latter (*Nebalia*) as may be more readily seen by comparing Fig. 7 with Fig. 10 (Plate VI). The molar region ("f" of textfigures 4 and 3, or "mo" of Figs. 7 and 10) is essentially the same in both Crustacea, but in the incisor region of *Mysis* (textfigure 4, or Fig. 7) the following parts become differentiated. The distalmost portion or apex of the mandible proper retains its character of an incisor region (labeled "c" in textfigure 4, or "in" in Fig. 7), but the processes below it (*i.e.*, "g" of textfigure 4, or "gf" of Fig. 7), called the gnathofimbrium, may assume the character of a fringe of setæ-like structures, which are quite long and slender in the Crustacea shown in Figs. 4, 2, etc., of Plate VI. The function of this fringe is probably to sweep the food into the mouth cavity, or to prevent the comminuted food from falling out of the mouth when the mandibles are working. The so-called lacinia mobilis, labeled "h" in textfigure 4, or "lm" in Figs. 7, 4, etc., is probably formed by the fusion of flattened seta-like structures like those forming the gnathofimbrium below it. The articulatory region which bears the articulatory condyle near the letter "a" in textfigure 4 bends outward more markedly in *Mysis* (textfigure 4) than in *Nebalia* (textfigure 3) and this tendency is quite pronounced in the following stages.

In the stage of the evolution of the mandibles represented in textfigure 5 (compare also Fig. 3, Plate VI) the profile of the black-margined region from "a" to "c" is not quite so arched as in textfigure 4, and this straightening out of the arch is apparently correlated with the "upward" growth of the incisor process (*i.e.*, the stippled area in textfigure 5) which becomes long and slender in *Apscudes* (textfigure 5, or Fig. 3), *Diastylis*, and other related forms. The gnathofimbrium "g" of textfigure 5 (or "gf" of Fig. 3) is much reduced in *Apscudes* (textfigure 5), and the lacinia mobilis "h" of textfigure 5 (or "lm" of Fig. 3) is relatively small and unim-

portant in *Apscudes*. There is also a marked tendency toward the reduction of the palpus "en," and, in fact, the palpus is completely lost in the Crustacea shown in Figs. 2 and 6; and the condition exhibited by the crustacean shown in Fig. 6 (Plate VI), which has not only lost its mandibular palpus, but also has no gnathofimbrium or lacinia mobilis (i.e., the structures labeled "en," "gf" and "lm" in Fig. 3, Plate VI) is very suggestive of that exhibited by the insect representing the next stage in the evolution of the mandible.



Textfigure 7. First parapodium of *Laodice rubra* (gill "cp" is present in the second parapodium, not the first). Textfigure 8. First thoracic limb of crustacean, based on condition found in *Syncarida*.

As was mentioned above, the mandible of the crustacean shown in Fig. 6 (Plate VI) is more like that of the insect shown in Plate VI, Fig. 5 (or in textfigure 6) than is true of the mandible of the crustacean figured in textfigure 5, since *Verbins* (Fig. 6) has lost its mandibular palpus, and has only the incisor process "in" and molar process "mo" in the distal region of the mandible—as is also true of the insect shown in Fig. 5. On the other hand, it is a very simple matter to compare the parts of the mandible of the insect shown in textfigure 6 (which is the same insect as that shown in Fig. 5, Plate VI) with the preceding crustacean stage shown in textfigure 5, and it is preferable for the sake of comparison, to use a crustacean in which the mandibular palpus is still retained, in order to demonstrate that there is no part of the insect's mandible comparable to the mandibular palpus of the crustacean.

In comparing the mandible of the insect *Machilis* (textfigure 6) with that of the crustacean *Apscudes* (textfigure 5) it may be seen

that, as we pass over into the insectan type, the basignath, or basal region of the mandible included between the points "a," "b" and "c," becomes somewhat slenderer and more elongate, and the outline of the black-margined area from "a" to "c" is less sinuate. An impressed line extending from "b" to "c" (compare also Fig. 5, Plate VI) is continued around the other side of the mandible and demarks the basal region, or basignath, from the distal portion of the mandible, or the distignath. The secondary nature of this subdivision of the mandible, is clearly evident if we trace back the evolution of the basal segment of the mandibular limb through the various stages from textfigure 6 to textfigure 1; so that it should be patent to anyone that the mandible of the insect shown in textfigure 6 represents a *single* segment of the original mandibular appendage, and any attempt to compare the parts of an insect's mandible (which is composed of only one segment of a limb) with the parts of the "body" of an insect's maxilla (which is composed of *at least two* segments of a limb) is wholly unjustified.

The incisor process of *Machilis* (*i.e.*, the stippled region from "d" to "e" in textfigure 6) is clearly the equivalent of the incisor process of *Apsendes* (*i.e.*, the stippled region from "d" to "e" in textfigure 5), and it is consequently merely a differentiated portion of the masticatory region of the mandible of *Mysis* (*i.e.*, the region from "f" to "e" in textfigure 4) in no wise comparable to the mandibular palpus "*en*" of textfigures 5, 4, 3, etc., as Heymons would maintain is the case with the incisor process of immature Ephemera, nor can the incisor process of *Machilis* (*i.e.*, the stippled area from "d" to "e" in textfigure 6) be compared to the exopodite of a biramous limb (*i.e.*, "*ex*" of textfigure 1) as Wood-Mason would maintain is the case! The lacinia mobilis "*h*" and the gnathofimbrium "*g*" of the mandible of the crustacean shown in textfigure 5, are lost in the mandible of the insect shown in textfigure 6; but this is not surprising, since these structures are frequently absent even in the Crustacea themselves (*e.g.*, in the crustacean mandible shown in Fig. 6, Plate VI). The molar process "*f*" of the insect's mandible shown in textfigure 6 is clearly homologous with the molar process "*f*" of the crustacean's mandible shown in textfigures 5, 4, and 3, and is consequently merely a differentiated portion of the masticatory

surface (or the gnathobase) of the basal segment of the mandibular appendage. On this account Wood-Mason's statement that the molar process "f" of *Machilis* (textfigure 6) represents the endopodite "en" of textfigures 5, 4, 3, 2, and 1, is most astounding, and it is very difficult to understand how anyone who has studied the Crustacea at all, could come to such an unwarranted conclusion.

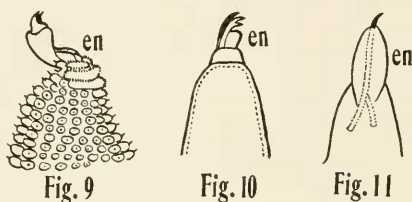
INTERPRETATION OF PARTS OF AN INSECT'S MANDIBLE.

From the foregoing discussion, it should be evident that an insect's mandible represents only one segment of the original limb forming the mandibular appendage of trilobites, Crustacea, etc., and neither the exopodite "ex" of textfigure 1, nor the endopodite "en" of textfigures 1, 2, 3, 4, and 5, are represented in the mandible of an insect. Furthermore, the division of *Machilis'* mandible into a basal region or basignath, and a distal region or distignath, by the suture from "b" to "c" in textfigure 6, is a purely secondary one, and in fact is foreshadowed in the mandibles of certain Crustacea such as our common southern shrimp (and a hint of this division is shown in the mandible of the crustacean *Ligia*—see Fig. 36, Plate VIII).

The evolution of the mandibles shown in textfigures 1, 2, 3, 4, and 5, is in complete agreement with the relative positions assigned the arthropods in question from their general anatomical features, and I do not see how anyone can deny that the series in all probability represents the stages through which a specialized mandible such as that of *Apseudes* (textfigure 5) has passed in assuming its present condition. We are therefore justified in assuming that the mandible proper (i.e., exclusive of the palpus) of Crustacea is composed of one and only one segment of the original mandibular appendage; and if we compare the tentorio-basignathal muscles attached to the basal region (basignath) of *Machilis'* mandible (Fig. 5, Plate VI) with the muscle attached to the base of the mandible of the crustacean shown in Fig. 2 (Plate VI) it is evident that the muscles are practically the same—consequently the regions to which they are attached are homologous, and the apparent basal segment of *Machilis'* mandible (Fig. 5) is therefore merely the basal region of the mandible of the crustacean shown in Fig. 2, which is composed of only one segment. It follows from this, that the subdivision of the mandible of *Machilis* is

purely secondary, and I am of the opinion that the apparent segmentation of the mandibles of "myriopods" is also purely secondary.

As we trace the modifications of the mandibles from textfigure 6 back to textfigure 1, it is evident that the incisor process (*i.e.*, the stippled area in textfigure 6) and the molar process "f" of the insect's mandible shown in textfigure 6 are merely differentiated portions of the gnathobase "gb" of the basal segment of the biramous



Textfigure 9. Diagram of limb of *Peripatus*. Textfigure 10. Diagram of limb of a tardigrade based on *Macrobotus*. Textfigure 11. Diagram of limb of a myzostomarian such as *Myzostoma cirriferum*.

mandibular limb shown in textfigure 1. If the lacinia of an insect's maxilla represents the endite or gnathobase "ci" of one segment of a mouthpart limb ultimately derived from a primitive limb of the type shown in Figs. 20 and 19 (Plate VII), while the galea of the maxilla represents the endite "ci" of another segment of such a limb (as I am hoping to demonstrate is the case, in a later article), then the incisor region and molar region together (*i.e.*, the differentiated portions of a gnathobase) of an insect's mandible would correspond to the lacinia (*i.e.*, a modified endite or gnathobase) of the maxilla. If this is true (as I am convinced is the case) it is absurd to attempt to homologize the small lacinia mobilis "h" (textfigure 4) of an insect's mandible (in other words, a small appendage of the gnathobase region formed by the fusion of a few setæ or spines) with the entire lacinia of an insect's maxilla (*i.e.*, with an entire gnathobase or endite) as is done by Chatin, and many other entomologists who are apparently ignorant of the true character of the parts they seek to compare.

The incisor region "c," the lacinia mobilis "h," the gnathofimbrium "g" and the molar region "f" of the crustacean mandible shown in textfigure 4 are all represented in the mandibles of certain

insects. The so-called prostheca of the mandibles of certain insects is possibly the homologue of the lacinia mobilis "h" of the mandible shown in textfigure 4, and from the discussion given above, it should be evident that it is impossible to homologize the prostheca or lacinia mobilis of an insect's mandible with the lacinia of an insect's maxilla, since the whole gnathobase, inclusive of the region from "f" to "e," of the segment forming the mandible shown in textfigure 4 is probably homologous with the whole gnathobase (or endite) which forms the lacinia of one of the segments entering into the composition of the body of the maxilla of an insect. If entomologists could only be brought to realize that the entire masticatory portion from "f" to "e" of a mandible such as that shown in textfigure 4 represents merely an area of one gnathobase (or endite) of one segment of a limb such as "gb" of textfigure 1, or "gb" of Fig. 20 (Plate VII), and that the lacinia of the maxilla represents a similar entire endite "gb" or "ci" of one segment of a limb such as that shown in Figs. 20 and 19, while the galea of the maxilla represents a second endite "ci" of another segment of such a limb (the terminal portion of the limb forming the maxillary palpus), there would not be such absurd proposals put forward as some of the interpretations of the parts proposed by Chatin,¹ Smith, Packard, Hollis, Wood-Mason, and others who have attempted to interpret the structure of insects' trophi in terms of crustacean anatomy.

The study of the modifications met with in the Crustacea has amply repaid the time spent upon it, and I would emphasize the fact that it is the Crustacea (not the Myriopoda) which have in each case

¹ Among other purely fanciful interpretations of the parts of the mandible of insects, Chatin, 1884, refers to "une ébauche de palpe" in the mandibles of certain staphilinid beetles, apparently influenced by the suggestion of Hollis, 1871, who regards the prostheca of the mandible of certain staphylinids, etc., as the representative of the mandibular palpus of Crustacea. Wood-Mason, 1879, has also developed the idea that the prostheca, or the lacinia mobilis of beetles represents the endopodite of a nauplius limb (Crustacea), and Eaton, 1883, in his "Monograph of the Ephemera" refers to the lacinia mobilis of the mandibles of immature may-flies as the representative of the endopodite of a formerly biramous limb. These and many similar misinterpretations of the parts of the mandible clearly show that it is necessary to study the evolution of the mandibular appendage in Crustacea, in order to properly interpret the parts of the mandible in insects.

furnished the key to the interpretation of the parts in insects; and, in fact, it is absolutely essential that anyone who desires to give the correct interpretation to the various structures of insects, and who wishes to determine the phylogenetic origin of insects, should give as much time as he is able to the study of the evolution of the parts in Crustacea, which have departed as little as any known forms from the types of arthropods ancestral to the "Myriopoda" and Insecta.

Machilis is an insect which is structurally much more primitive than most entomologists realize, and instead of being a degenerate winged insect as Handlirsch would have us believe, I would insist that it is absolutely primitive in most respects, and has departed in fact but little from the condition characteristic of some of the ancestral insects. It has even preserved certain characters suggestive of affinities with the primitive Collembola—although its closest affinities are with the *Lepisma-like* Apterygota, and it furnishes us with a connecting link anatomically annectant between the Crustacea and the *Lepisma-like* types, as well as with the lowest representatives of the winged insects such as nymphal Ephemera, etc. In fact, the mandibles of *Machilis* (and to some extent of certain immature ephemerids also) are more like the mandibles of Crustacea than they are like the mandibles of other insects (as is likewise true of the muscles attached to the mandibles of *Machilis*) and a study of the anatomical details of *Machilis* (and of nymphal ephemerids also) is absolutely essential in making an attempt to trace the evolution of the insectan type of arthropod. On this account, I have used *Machilis* to illustrate the probable mode of origin of one type of insectan mandibles; but it is also necessary in such a study to trace the origin of the type of trophi found in the Dicellura (*Japyx*, *Campodea*, etc.) as well, since the dicelluran type is one of the primitive types of insects as well as *Machilis*; but the Dicellura are of less importance despite their remarkable resemblance to the Symphyla (e.g., *Scolopendrella*, etc.) since their line of development, in paralleling that of the Symphyla, leads away from the main path of development followed by winged insects (as exemplified by immature ephemerids) and higher Crustacea, along a line of specialization having no particular bearing upon the developmental tendencies of insects in general. *Machilis*, *Lepisma*, and *Nicoletia*, on the other hand, exhibit

many tendencies carried over into winged insects through the ephemerid and plecopteran types, and since *Machilis* is the most primitive of these forms, it will serve as the starting point for the next of the series of papers in which it is proposed to trace the modifications of the mandibles met with in insects in general.

TYPES OF CRUSTACEAN MANDIBLES.

Since the Crustacea form the connecting link between the lower arthropods and the insectan and myriopodan types, it may be of some interest to note the modifications met with in the more important groups of Crustacea, which might throw some light upon the conditions occurring in the mandibles of insects. The condition met with in the mandibles of the lower forms such as the Copepoda (Fig. 30), Ostracoda (Fig. 33) and Branchiopoda (Figs. 22 and 23) is too far removed from the insectan type to be of much interest from this standpoint, especially since the incisor and molar regions are not clearly differentiated in these lower Crustacea. Similarly, the mandible of *Nebalia* (Fig. 10) is still too primitive to be of much value in such a study. *Mysis* (Fig. 7) on the other hand has approached sufficiently close to the type ancestral to insects, to exhibit a number of features such as the differentiation into incisor region proper, gnathofimbrium, and molar region, and the development of a lacinia mobilis, all of which are present in some insects. The mandibular palpus, however, is still very large in proportion to the size of the mandible proper.

In such Crustacea as *Stegocephalus* (Fig. 4) there is a pronounced reduction of the palpus "*en*," while the incisor region "*in*" becomes slenderer and more elongate, and the gnathofimbrium "*gf*" is of greater extent and is composed of seta-like structures forming a hair-like fringe rather than a cluster of spine-like projections as in *Mysis* (Fig. 7). In the species of *Asellus* shown in Fig. 1, the mandibular palpus "*en*" is quite reduced; but the incisor region "*in*" is not quite as long as in *Stegocephalus* (Fig. 4). The gnathofimbrium "*gf*" is of somewhat less extent than in Fig. 4, and the reduction of the gnathofimbrium "*gf*" is carried still further in Fig. 3.

In *Diastylis* (Fig. 2) the mandibular palpus has completely disappeared, and the incisor process is rather slender and greatly

elongate. The gnathofimbrium "*gf*" is well developed and is composed of flattened seta-like processes. The lacinia mobilis "*lm*" is somewhat reduced, but is still of a different character from the seta-like components of the gnathofimbrium "*gf*," although in the mandibles shown in Figs. 1 and 3, the lacinia mobilis "*lm*" does not differ greatly from the structures composing the gnathofimbrium "*gf*."

In the decapod shown in Fig. 6, the mandibular palpus has become atrophied, and the beginning of the process is shown in the decapod depicted in Fig. 35, in which the mandibular palpus "*en*" is merely a small rudimentary appendage of the greatly developed mandible proper. The incisor process "*in*" of the decapod shown in Fig. 6 is not very large, and it has completely disappeared in the decapod shown in Fig. 26, which has retained only the molar process "*mo*" of the distal structures of the mandible. The gnathofimbrium and lacinia mobilis have apparently not developed in the decapod types of Crustacea, though *Mysis* (Fig. 7) which resembles *Thysanopoda*, *Euphausia*, and other forms related to the Decapoda, has acquired a lacinia mobilis "*lm*," and a primitive sort of gnathofimbrium "*gf*."

In the mandible of *Squilla* (Fig. 28) the palpus "*en*" is very small, and the structure which I have interpreted as the molar process "*mo*" is folded back in a peculiar fashion. The incisor region "*in*" is continued basalward in a region which may be the precursor of the gnathofimbrium of higher forms. At any rate, the incisor surface is of greater extent than in the higher forms.

In the mandibles shown in Figs. 25 and 32, there is a peculiar gnathofimbrial lobe "*gf*," and the molar process "*mo*" has taken on a peculiar form, and is somewhat folded around in a fashion suggestive of the process which has been carried to an extreme in the molar process "*mo*" of Fig. 28. Just above the base of the mandibular palpus "*en*" in Fig. 25, is a small protuberance which is produced into two tooth-like processes just above the base of the cut-off mandibular palpus in Fig. 32. These tooth-like processes may be the precursors of the elongate incisor "tusks" of the mandibles of certain ephemerid nymphs, or a process of the region "*in*" of Fig. 4 forms the tusk-like process of the mandibles of ephemerid nymphs.

The mandible of a male of *Gnathia* (Fig. 27) resembles the

mandibles of certain insects in having no palpus, or molar region differentiated from the incisor region. On the other hand, the mandible of *Caprella* resembles that of certain insects in having a short molar protuberance "mo," and a shorter and stouter type of mandible than is present in many Crustacea. The tendency toward a shortening of the mandible is also exhibited by *Ligia* (Fig. 36) and other isopods, and the molar process "mo" becomes blunter and stouter in *Ligia*. Through a further shortening and through the reduction of the basignath, or basal region of the mandible shown in Fig. 36, the type of mandible found in certain pterygotan insects might easily be derived, and the question naturally arises as to whether the small sclerite called the basimandibula (or the "trochantin" of the mandible) which is situated at the base of the mandible in certain orthopteroid insects, may not correspond to the demarked basal region of a mandible such as that shown in Fig. 36, in which there is a slight indication of a division of the mandible into a basal and a distal portion by the transverse dotted line shown in the figure. While I would not deny the possibility of such an explanation of the basimandibula (or mandibular "trochantin") in insects, I am more inclined to regard the formation of this basal sclerite or basimandibula as the result of a chitinization of the articulatory membrane at the base of the mandible in insects.

RELATIONSHIPS INDICATED BY MANDIBULAR APPENDAGE.

As was stated at the beginning of this paper, the mandibles alone can furnish but a small portion of the evidence of relationship, which must be drawn from as many sources as possible, and should include not only the study of anatomical details, but also that of the embryological development of the forms in question, as well as their habits, immature stages, and all other features having a direct bearing upon the subject. Taken in connection with these other features, however, the nature of the mandibular appendage in the various arthropodan groups is of considerable value in determining the lines of development and the interrelationships of these groups, and it may be of interest to point out some of the indications of relationship between certain of the groups furnished by an examination of the mandibles.

The character of the mandibular limb (or any of the mouthpart

limbs) of a trilobite such as that shown in Fig. 9 is more like that of the mouthpart limbs of the merostomes (Figs. 12, 8, etc.) than it is like the mandible of a crustacean, as was pointed out above, and in addition to the similarity in the head region, and in the body segmentation and the pygidial region of an immature merostome such as *Limulus* and certain of the Trilobita, this resemblance might justify our grouping the trilobites with the merostomes, etc., in the subphylum "Podognathata," rather than with the Crustacea and their allies, in the subphylum "Eugnathata." The gnathobase "*gb*" of a trilobite such as that shown in Fig. 18 is very similar to the gnathobase "*gb*" of the merostome shown in Fig. 12, and the appendage homologous with the mandibular appendage of Crustacea, etc., is more like a walking leg in the trilobites, merostomes, and their allies, than it is like a true mandible (such as the mandible of a crustacean), so that the evidence of the mandibular appendage of trilobites and merostomes would indicate a somewhat closer relationship between these two groups than between the trilobites and Crustacea, although the trilobites are clearly intermediate between the Crustacea and Merostomata, and are but slightly nearer the one than the other.

In the eurypterid shown in Fig. 17, there is a small appendage "*ci*" called the "epicoxite" by Clarke and Ruedemann, 1912, which is situated immediately below the gnathobase "*gb*" of the fourth "endognathite" (or mesal region of the basal segment of the limb) according to Clarke and Ruedemann. In the limb of the xiphosuran *Limulus* shown in Fig. 14, I find a similar structure "*ci*" situated below the gnathobase "*gb*," and if the structure "*ci*" of Fig. 14 is homologous with that labeled "*ci*" in Fig. 17 (as seems to be the case) the presence of this peculiar structure in both eurypterids and xiphosurans would further strengthen the view that the two groups are extremely closely related.

Since the Scorpionida are apparently descended from forms resembling the Eurypterida and other merostomes, I have tried to find the homologues of the gnathobases "*gb*" of Figs. 15 and 12, in a scorpion's limb and I would suggest that the small projection labeled "*gb*" in the basal segment of the limb of the scorpion shown in Fig. 16 may correspond to the gnathobases "*gb*" of Figs. 15 and 12.

The gnathobases "*gb*" of the merostomes shown in Figs. 12 and 16 are clearly homologous with the gnathobases "*gb*" of the trilobites shown in Figs. 18 and 9, since in each instance the gnathobase is formed by a mesal prolongation of the entire basal segment of the limb. On the other hand, the so-called gnathobases "*gb*" of certain Crustacea such as those shown in Figs. 13 and 21, appear to be slightly different outgrowths or appendages of the segment; and in the crustacean shown in Fig. 20, the endites "*ei*" of the several segments of the limb, which are homologous with the gnathobase or endite labeled "*gb*" in the basal segment, have taken on the appearance of segmented appendages of the segments rather than mesal prolongations of the entire segment—although it must be admitted that the endite "*gb*" of the basal segment of the limb shown in Fig. 20, approaches more closely to the trilobitan type of gnathobase ("*gb*" of Fig. 18). The greater similarity between the gnathobases of trilobites and merostomes (*i.e.*, "*gb*" of Figs. 18, 15, and 12) than between the gnathobase of trilobites and the endites of Crustacea in general (compare "*gb*" of Fig. 18 with "*gb*" of Figs. 21 and 13, or "*ei*" of Figs. 19 and 20), however, would tend to throw the trilobites slightly nearer the merostomes than the Crustacea, when taken into consideration with certain other features of resemblance in the groups Trilobita and Merostomata.

As was remarked above, the mandibles of the Branchiopoda (Figs. 22 and 23) are not very much like the mandibular appendage of trilobites (Fig. 9) despite the close relationship between the two groups; but the mandibles of the Copepoda and Ostracoda (Figs. 30 and 33) have still retained both the exopodite "*ex*" and the endopodite "*en*" of a typical biramous limb (Fig. 9, "*ex*" and "*en*"), and it would appear that the masticatory portion of the mandible of the Crustacea shown in Figs. 30 and 33 represent true gnathobases "*gb*" of a trilobitan limb (Fig. 9) since the structures in question are mesal prolongations of the entire basal segment in both instances. I would therefore maintain that the Copepoda (and the Ostracoda also) are quite closely related to the Trilobita, although the former belong to the subphylum "Eugnathata" in which the mandibles have passed beyond the walking-leg stage and have become true jaws; while the trilobites appear to be somewhat more closely associated with the subphylum "Podognathata" in which the appendage homo-

logous with the mandibles of Crustacea are more limb-like, or are not of the true "jaw" type.

The fact that the incisor process "in" of *Nebalia* (Fig. 10) is but weakly developed, and the differentiation of the masticatory region is consequently not so marked as in the higher forms, would indicate that *Nebalia* is a comparatively primitive type but little higher than the Branchiopoda, Copepoda, etc.; while the fact that *Nebalia* exhibits a marked tendency toward a differentiation of the masticatory area and the development of an incisor process (even though a feeble one), shows that *Nebalia* is structurally intermediate between the lower Crustacea and the more modified forms, as is borne out by the character of the body in general. The great size of the mandibular palpus (in comparison with the size of the basal segment of the limb which forms the mandible proper) and its apparent ability to function in locomotion, is another feature indicating the comparatively primitive character of *Nebalia*, and the evidence of the mandible is in full accord with other indications of the intermediate position of *Nebalia* as a form connecting the lower Crustacea (Branchiopoda, Copepoda, Ostracoda, etc.) with the more modified types. *Nebalia* has not developed a lacinia mobilis (and gnathofimbrium), and on this account the absence of a lacinia mobilis in the mandibles of certain Crustacea may possibly be regarded as somewhat more primitive condition than is the case with those Crustacea in which the lacinia mobilis is developed.

The Euphausiacea, such as *Thysanopoda*, are very primitive types related to the Decapoda, and since both of these orders have not developed a lacinia mobilis (see Fig. 35) in the mandible (and the gnathofimbrium is usually lacking also), this fact would support the view that the Decapoda and Euphausiacea are quite closely related. The Stomatopoda such as *Squilla* (Fig. 28) are rather primitive forms in some respects, and their mandibles also lack the lacinia mobilis as in the Euphausiacea and Decapoda, which they resemble in certain other anatomical features as well.

The Mysidacea such as *Mysis* (Fig. 7) have developed a lacinia mobilis "lm," and a primitive sort of gnathofimbrium "gf," and in this respect they resemble the Cumacea (Fig. 2), Tanaidacea (Fig. 3), Isopoda (Figs. 1 and 36) and related forms, as was first pointed out

by Boas, 1882. Calman and other recent carcinologists have removed the Mysidacea from the old order Schizopoda which also included the Euphausiacea, etc., and have grouped the Mysidacea with the Cumacea, Tanaidacea, Isopoda, etc., because of the presence of the lacinia mobilis (among other features) in these forms and its absence in the Euphausiacea and Decapoda. I cannot avoid the conclusion that the Mysidacea are much nearer the Euphausiacea, however, despite these facts, although the Mysidacea are evidently intermediate between the Euphausiacea on the one side, and the Cumacea, Tanaidacea, Isopoda, etc., on the other. It is thus a matter of determining the closest affinities of the Mysidacea and not a question of their intermediate character, which is to be decided; and while the evidence of the mandibles would support the view that the Mysidacea are somewhat nearer the Cumacea, Tanaidacea, etc., I am by no means satisfied that other points of resemblance between the Mysidacea and Euphausiacea are not of greater importance.

The mandibles of the Syncarida such as *Anaspides* have no lacinia mobilis; but a gnathofimbrial lobe very suggestive of that shown in Fig. 25, "*gf*," occurs on the mandible of *Anaspides*, and, contrary to the opinion of Calman, I would maintain that the Syncarida are nearer the types ancestral to the Tanaidacea, Isopoda, etc., than they are accredited to be by Calman and other carcinologists. In fact, it is quite probable that the common ancestors of the Tanaidacea, Isopoda, Amphipoda, Insecta and Symphyla, etc., were anatomically intermediate between the Syncardia on the one side, and the Mysidacea on the other and were related to the Arthropleura and Oxyuro-poda as well; but this matter will be discussed more at length in a later paper.

The mandible of a cumacean such as *Diastylis* (Fig. 2) bears a well developed gnathofimbrium "*gf*" and a lacinia mobilis "*lm*," and in the development of its incisor process, it resembles *Apsudes* (Fig. 3). The Cumacea are regarded by Calman as intermediate between the Mysidacea and the isopod type of higher Crustacea, and a study of the mandible would lend weight to this view. On the other hand, the Cumacea are such highly aberrant forms, that they do not furnish any very valuable clues as to the phylogeny of the higher Crustacea. Their type of mandible, however, is as near that

of the Tanaidacea, Isopoda and Amphipoda as any, and it is more logical to group them with these forms than to place them lower in the scale of development than the Mysidacea, as was formerly done by the earlier carcinologists.

The mandibles of the Isopoda (Figs. 1 and 36) and Tanaidacea (Fig. 3) are remarkably similar, and both are very like those of the Amphipoda (Fig. 4), and the resemblance on the part of the mandibles thus further substantiates the evidence of a very close relationship between these groups drawn from other sources. All of these groups are apparently closely related to insects, and with the exception of the presence of the mandibular palpus, the types of mandibles occurring in these forms are approached by the mandibles of certain insects some of which are members of even so high a group as the Pterygota. It would thus appear that certain hereditary impulses from the Crustacea have surged upward, so to speak, through the apterygotan lines of descent and have penetrated well into the lines of descent of the pterygotan insects before losing their force and becoming so greatly modified as to be no longer recognizable as crustacean features.

It should be borne in mind, that there are several types of mandibles present in insects, which can be traced back to crustacean types, and the type of mandible shown in textfigure 6 (which was probably derived from the crustacean type shown in textfigure 5) is only one of these. The type of insectan mandible shown in textfigure 6, however, is so much like that of the crustacean shown in textfigure 5, that it is almost more crustacean than it is insectan, despite the fact that the insect (*Machilis*) to which it belongs, is indisputably an "out-and-out" hexapod. The character of the head and its appendages (Maxillary palpus, etc.) in *Machilis*, the nature of its body, and many other features than its mandibles alone, proclaim its close relationship to the Crustacea; and if *Machilis* is nothing but a degenerate winged insect (instead of being a very primitive type near the ancestors of winged insects) as Handlirsch, 1909, would have us believe, then the Crustacea, to which *Machilis* is so closely related, must also be regarded as degenerate winged insects (!) because *Machilis* is anatomically much nearer the Crustacea than winged insects are—and if this be a sign of degeneracy, then the Crustacea must be degenerate winged insects also.

I suspect that Handlirsch's overweening desire to derive winged insects directly from trilobites is the cause of his attempt to deny to *Machilis*, *Lepisma* and related *Apterygota* their rightful positions as the nearest known representatives of the *precursors* of winged insects, and to relegate them to the subordinate position of mere "degenerate" winged insects, for there is a wide gap between these *Apterygota* and the trilobites and they do not seem to approach the trilobitan type any more closely than the winged insects themselves do—and if winged insects are to be derived directly from trilobites, their precursors must perforce resemble trilobites more closely than winged insects do! Therefore, in order to maintain his unfounded theory that winged insects are descended directly from trilobites, it was necessary for Handlirsch to sweep the true ancestral types of insects aside as degenerate winged insects, since they do not fit into his preconceived scheme of the origin of pterygotan insects. As an anatomist, however, I cannot avoid the conclusion that such *Apterygota* as *Machilis*, *Lepisma*, *Nicolletia*, *Campodea*, etc., are far more primitive than winged insects (as is also shown by the embryological development of these forms) and if the facts of the case do not fit into one's theory, it is much better to discard the theory and stick to the facts!

I have perhaps laid greater emphasis upon Handlirsch's views as to the origin of winged insects, than should be given to a theory which was evidently developed merely as a side issue of his monumental work on fossil insects; but so many recent writers, who have not taken the trouble to go into the matter at all deeply, have set forth this unfounded view of Handlirsch's (even in text-books) as though it were absolutely demonstrated, that it is high time that someone should call attention to the many obstacles in the way of accepting such a view. There are many other insuperable obstacles to the acceptance of the view that winged insects (or even the most primitive of the apterygotan types which preceded winged insects) may be derived directly from trilobites; but since this paper deals with the mandibles alone, I shall confine myself to the evidence offered by these structures—which is quite sufficient in itself to disprove Handlirsch's theory, since the mandibles clearly indicate that there must have been a great number of intermediate stages between so primitive

a type as the biramous mandibular limb shown in textfigure 1 and the greatly modified single segment of such a limb which forms the mandible of the primitive insect shown in textfigure 6.

Let us for a moment consider the tremendous changes involved in such a leap directly from the type of mandibular limb shown in textfigure 1 to the type of mandible shown in textfigure 6, without reference to any of the intermediate stages of the series at whose extremes these types stand. The most "spectacular" change would be the immediate loss of the exopodite "cr" and the endopodite "en" which are better developed in trilobites than in other arthropods, and represent the extreme of primitiveness as exhibited by the trilobite's mandibular limb. The endopodite "en" is relatively larger and better developed in trilobites than is shown in textfigure 1 (compare with correct proportions shown in Fig. 9 of Plate VI) and it still functions as a locomotor appendage in these forms. That such a well developed, perfectly functioning, and apparently useful structure as this endopodite (which is wholly wanting in all insects) should suddenly and completely disappear without first *gradually* becoming reduced to fewer segments and losing its importance as a functioning organ of any value (as is shown in the complete series from textfigure 1 to textfigure 6) is extremely improbable, to say the least; and it would require more of a mutational leap than even the famous *Drosophila* has been able to execute, to accomplish "all in one fell swoop" not only the loss of the exopodite and greatly developed endopodite, but the profound modification and intricate differentiation of the parts of the basal segment which would transform the gnathobase of a trilobite into the highly specialized mandible of an insect!

It should be borne in mind that textfigure 1 is a diagram pure and simple, and consequently the trilobite's gnathobase "gb" as shown in textfigure 1 is not as much differentiated as the diagram would indicate (since the series shown in the textfigures is intended to emphasize certain points of development thereby making it more readily comprehensible as to how the changes have probably taken place); and, as one may see by referring to Fig. 9 (Plate VI) the basal segment of the mandibular limb is still comparatively small in the trilobite, and its gnathobase "gb" merely bears a few spine-like pro-

jections. It is a considerable leap from such a condition even to the weakly developed type of mandible shown in textfigure 3 (which is infinitely more primitive than any insect's mandible), since in the latter form, there is a small incisor process "e" distinct from the molar process "f" (neither of which are present in the trilobite), and the basal segment of the limb has begun to take on a contour suggestive of a mandible—while the basal segment of the trilobite's mandibular limb is just like the basal segment of its "walking" legs; and the leap from such a basal segment to one of the mandibular type bearing not only an incisor process, but a lacinia mobilis, molar process, and other complicated structures, such as occur in the mandibles of immature ephemerids (whose mandibles are the most primitive of any winged insect thus far studied) involves such profound and fundamental changes in structure, that if we had only the evidence of the mandibles alone, to judge from, it would be impossible to justify Handlirsch's impossible claim that winged insects (or even the far more primitive apterygotan insects) were derived directly from trilobites; and it is indeed astounding that such revolutionary claims have been so readily accepted by scientific men who are usually more than "conservative" in accepting new views which are not demonstrated by almost irrefutable facts!

The nature of the mandibular appendages, in addition to the evidence drawn from many other sources, would indicate that the "higher" Crustacea, (*i.e.*, Amphipoda, Isopoda, Tanaidacea, etc.) together with the Insecta and Symphylo-Pauropoda, were in all probability derived from common ancestors anatomically intermediate between the Mysidacea on the one side and the Syncarida on the other, and these common ancestral types were probably also related to the Arthropleura and *Oxyuropoda* as well. Starting from this common source, the lines of descent of the Insecta were paralleled on one side by the "higher" Crustacea, and on the other by the lines of descent of the Symphylo-Pauropoda. The symphylian line of development paralleled that of the Insecta only as far as the point where the Dicellura (*Camptoda*, *Japyx*, etc.) were developed, whereupon the lines of development of the Symphyla and the Dicellura appear to become specialized in a direction which does not lead to the production of types approaching the winged insects. On the other hand, the

lines of descent of the higher Crustacea appear to parallel that of the insects for a much longer distance, even until the lower forms of winged insects were developed, since many crustacean characters are carried over into the lower types of winged insects such as the Ephemera, etc. The study of the anatomical features of the Crustacea is therefore of much greater importance than that of the "myriopods," and in the foregoing discussion, it has been shown that at least one type of insect mandible has been derived more or less directly from a type occurring in the Crustacea. The derivation of the other types of mandibles occurring in insects will be discussed in a second paper of this series, in which it is proposed to take up the evolution of the modifications met with in the different orders of insects as well.

SUMMARY.

The principal points brought out in the foregoing discussion may be briefly summarized as follows:

1. The parapodium of an annelid represents the probable precursor of the primitive biramous arthropodan limb, which in turn is the forerunner of the mandibular appendage of Crustacea, Insecta, and "Myriopoda."

2. Insects, myriopods, and Crustacea form a subphylum (the Eugnathata) in which the mandibular appendage is essentially jaw-like rather than limb-like. In the rest of the Arthropoda (which constitute the subphylum Podognathata) the limbs homologous with the mandibular appendage are not jaw-like, and trilobites appear to be slightly nearer the latter group than the former, although they are anatomically intermediate between the two groups.

3. The biramous mandibular appendage of trilobites, in which both exopodite and endopodite are retained, and in which the basal segment of the limb has become slightly modified for holding food through the development of a gnathobase, while the rest of the appendage still serves a locomotor limb, forms the starting point for tracing the modifications met with in the mandibular appendage of Crustacea, Insecta and "Myriopoda."

4. The first steps in the production of a true mandible from such an appendage are the loss of the exopodite, and the reduction of the endopodite to a mandibular palpus, accompanied by the greater de-

velopment of the basal segment of the mandibular appendage to form the body of the mandible proper, and the differentiation of the masticatory surface of the gnathobase into an incisor and a molar area.

5. In the mandibles of the Mysidacea and higher Crustacea, a lacinia mobilis is formed in the incisor region (*i.e.*, the region distal to the molar process) through the fusion of several hair-like or spine-like structures similar to those which form the so-called gnathofimbrium or bordering fringe of the region of the mandible immediately beyond (distal to) the molar process. These structures also occur in the mandibles of insects, but the homologue of the mandibular palpus of Crustacea has never been found in any insect thus far described.

6. The mandible of *Machilis* represents one type of insectan mandible which is even more crustacean than insectan in appearance, and the derivation of this type of mandible from a crustacean precursor involves so slight a change, that the evidence drawn from a study of the mandibles is in full accord with that drawn from other sources, which indicate that the Crustacea probably represent the forms ancestral to insects.

7. The character of the mandible of *Machilis* indicates that it is a very primitive form, and the many crustacean features preserved by *Machilis* clearly indicate that it is a much more primitive insect than it is generally supposed to be. This insect is anatomically annectant between the Crustacea and such apterygotan insects as *Lepisma*, *Nicoletia*, etc., which in turn lead to the lower types of winged insects such as the Ephemera, and through them and the Plecoptera to the remainder of winged insects. There is no reason whatsoever for the unfounded claim that *Machilis* is a degenerate winged insect, and it approaches the crustacean type so closely that if *Machilis* is to be regarded as a degenerate winged insect, then the Crustacea must also be regarded as degenerate winged insects.

8. It is utterly impossible to derive any insectan type of mandible directly from the trilobitan type of mandibular appendage, since the immediate loss of the exopodite and the endopodite (which still functions as a locomotor appendage in trilobites), the immediate assumption of the mandibular form by the comparatively simple basal segment

of the trilobite's mandibular limb, and the immediate differentiation of its gnathobase into a highly complicated apparatus including a specialized incisor region, a lacinia mobilis, a gnathofimbrium, and a specialized molar process, involve too profound and far reaching changes to be accomplished save by a gradual process of evolution involving a long series of intermediate stages.

9. The Crustacea not only approach the insectan type astonishingly closely, but they also furnish us with a long series of intermediate stages connecting the insectan types of structures with the lower arthropodan forms, such as the Trilobita. Furthermore, they not only furnish excellent connecting links between the Insecta and lower arthropods, but they are the *only forms* which furnish these intermediate types leading from the lower arthropods to the Insecta, and this fact is one which cannot be ignored in attempting to determine the character of the ancestors of insects.

10. The Crustacea not only furnish the intermediate stages leading from the lower arthropods to the insectan type, but they also furnish us with the key to the proper interpretation of the homologies of the various insectan structures, and they enable us to clear up many of the false views concerning the meaning of the parts of the mandibles as well as other structures of insects. Thus, a study of the evolution of the mandibular appendage in the Crustacea clearly shows that the incisor region, the lacinia mobilis, the gnathofimbrium and the molar process are merely differentiated portions of the masticatory surface of a gnathobase or endite, while a similar study of the appendages homologous with the maxillæ of insects indicates that the lacinia represents a complete endite (or "gnathobase") of one segment of a limb, while the galea represents a second endite of another segment of the limb, whose terminal segments form the maxillary palpus. It is thus impossible to homologize the lacinia mobilis of the mandible with the lacinia of the maxilla in insects; and since the mandible represent only one segment with its gnathobase, while the body of the maxilla represents at least two segments with their endites (or gnathobases) it is obviously incorrect to claim that the parts of the maxilla are repeated in the mandible, as is done by many entomologists.

11. A study of the mandibles, in connection with other features, would indicate that insects arose from ancestors which were an-

atomically intermediate between the Mysidacea and the Syncarida, and were also in all probability related to the Arthropleura and to *Oxyuro-poda* as well. From this common ancestry arose the higher Crustacea, whose lines of development have paralleled that of insects on one side, and the Symphylo-Pauropoda, whose lines of development have paralleled that of insects on the other side. The lines of development of the higher Crustacea have accompanied those of the insects much further than the lines of development of the Symphylla, etc., have, and many crustacean features have even been carried over into the lower representatives of the winged insects.

BIBLIOGRAPHY.

1896. BEECHER. The Morphology of Triarthrus. Amer. Jour. Sci., 16, p. 166.
 1882. BOAS. Verwandtschaftsbeziehungen der Malakostraken. Morph. Jahrb., 8, p. 485 (also "Zoologie").
 1909. BOERNER. Neue Homologien zwischen Crustaceen und Hexapoden. Zool. Anz., 34, p. 100.
 1917. BORRADAILE. The Mouthparts of Palemonid Prawns. Proc. Zoöl. Soc. London, 1917, p. 37.
 1909. CALMAN. Article "Crustacea," in Lankaster's Treatise on Zoölogy.
 1903. CARPENTER. Relationships between the Classes of Arthropods. Proc. Roy. Irish Acad., 1903, p. 320.
 1884. CHATIN. Morphologie Comparee des Pieces Maxillaires, Mandibulaires et Labiales chez les Insectes Broyeurs.
 1912. CLARKE & RUEDEMANN. Eurypterida of New York. N. Y. State Educat. Dpt. Mus. Memoir No. 14.
 1919A. CRAMPTON. Evolution of Arthropods with Especial Reference to Insects. Amer. Nat., 53, p. 143.
 1919B. CRAMPTON. Article on the Ancestry of Insects in the 51st Rpt. of the Ent. Soc. of Ontario for 1919.
 1900. FOLSOM. Mouthparts of Anurida. Bull. Mus. Comp. Zoöl. Harvard, Vol. 36, p. 87.
 1909. HANDLIRSCH. Die Fossilen Insekten.
 1896. HEYMONS. Entwicklung und Koerperbau von Odonaten und Ephemeroïden. Anh. Abh. Kgl. Preuss. Akad. Wiss. Berlin, 1896.
 1901. HEYMONS. Entwicklungsgeschichte der Scolopender. Zoologica, 13, p. 1.
 1872. HOLLIS. Homologue of the Mandibular Palp in Certain Insects. Jour. Anat. and Physiol., 6, p. 395.
 1917. LULL. Organic Evolution.
 1898. PACKARD. Entomology.
 1920. RAYMOND. Trilobites as Ancestors. Amer. Nat., 54, p. 398.

1916. RUEDEMANN. Median Eye in Trilobites. Proc. Nat. Acad. Sci., 2, p. 234.
1915. SCHUCHERT. Textbook of Geology.
1892. SMITH. Mouthparts of Copris with Notes on the Homologues of the Mandibles. Trans. Amer. Ent. Soc., 19, p. 83.
1916. TOTHILL. Ancestry of Insects. Amer. Jour. Sci., 42, p. 373.
1911. WALCOTT. Middle Cambrian Merostomata. Smithsonian Misc. Coll. 57, No. 2, p. 19.
1912. WALCOTT. Middle Cambrian Banchiopoda, etc. *Ibid.*, No. 6, p. 148.
1879. WOOD-MASON. Morphological Notes Bearing on the Origin of Insects. Trans. Ent. Soc. London, 1879, p. 145.

ABBREVIATIONS.

- a* Basal condyle; "a" and "b" denote limits of points of attachment of mandible.
- b* "a" and "b" denote extent of basal attachment of mandibular appendage.
- bg* . . . basignath, or basal region of mandible.
- c* distal limits of basignath on outer surface of mandible.
- ci* appendage called epicoxite in merostome gnathobase.
- d* point at base of incisor process.
- dg* . . . distignath, or distal region of mandible.
- c* apex of mandible.
- ei* endites, or gnathobase (also called endognathite); ventral cirrus of annelid parapodium.
- en* endopodite or inner branch of biramous limb; main axis of annelid parapodium.
- ep* epipodites or gills.
- ex* exopodite or outer branch of biramous limb; dorsal cirrus of annelid parapodium.
- f* molar process.
- g* gnathofimbrium.
- gb* gnathobase or endite of basal segment of limb.
- gf* gnathofimbrium, or marginal fringe in distal region of mandible.
- h* lacinia mobilis or epignath.
- in* incisor process or incisor region (incisorium).
- lm* lacinia mobilis or epignath.
- mo* molar process or mola.

EXPLANATION OF PLATES VI, VII, VIII.

Unless otherwise specified, all figures represent posterior views of right mandibular appendage so oriented that apex is directed toward the top of the page, and region normally bearing endopodite or palpus, is directed toward the left-hand margin.

PLATE VI.

- Fig. 1. Mandible of *Asellus communis* (Isopod Crustacea).
 Fig. 2. Mandible of *Diastylis* sp. (Cumacean Crustacea).
 Fig. 3. Mandible of *Apscudes spinosus* (Tanaidacean Crustacea).
 Fig. 4. Mandible of *Stegocephalus* sp. (Amphipod Crustacea).
 Fig. 5. Mandible of *Machilis* sp. (Apterygotan Insecta).
 Fig. 6. Mandible of *Verbius zostericola* (Decapod Crustacea).
 Fig. 7. Mandible of *Mysis stenolepis* (Mysidacean Crustacea).
 Fig. 8. Swimming leg of young *Limulus polyphemus* (Xiphosuran Merostomata).
 Fig. 9. Mandibular appendage of opisthoparian trilobite, *Triarthrus becki*, based on figure by Raymond.
 Fig. 10. Mandible of *Nebalia bipes* (Leptostracan Crustacea).

PLATE VII.

- Fig. 11. Basal region of swimming leg of immature *Limulus polyphemus* (Xiphosuran Merostomata).
 Fig. 12. First gnathopod of *Limulus polyphemus* (Xiphosuran Merostomata).
 Fig. 13. First thoracic limb of the branchiopodan crustacean, *Limnadia lenticularis*, based on figure by Sars.
 Fig. 14. Gnathobase of third gnathopod of *Limulus polyphemus* (Xiphosuran Merostomata).
 Fig. 15. Swimming leg of eurypteridan merostome, *Eusarcus*, based on figure by Clarke and Ruedemann.
 Fig. 16. Base of leg of *Scorpio* sp. (Scorpionidan Arachnida).
 Fig. 17. "Coxa of fourth left endognathite seen from below" of eurypteridan merostome, taken from figure by Clarke and Ruedemann.
 Fig. 18. Fourth thoracic limb of opisthoparian trilobite, *Neolenus*, based on figure by Walcott.
 Fig. 19. Sixth or seventh limb of *Apus* sp. (Branchiopodan Crustacea).
 Fig. 20. First limb of *Apus* sp. (Branchiopodan Crustacea).
 Fig. 21. First thoracic limb of syncaridan crustacean, *Paranaspides lacustris*, from figure by Smith.

PLATE VIII.

- Fig. 22. Mandible of *Apus productus* (Branchiopodan Crustacea).
 Fig. 23. Mandible of *Branchippus vernalis* (Branchiopodan Crustacea).
 Fig. 24. Mandible of *Apus productus*—same as Fig. 22, but in position normally assumed when *in situ*.
 Fig. 25. Mandible of *Conilera cylindracea* (Isopodan Crustacea).
 Fig. 26. Mandible of *Crangon vulgaris* (Decapodan Crustacea).
 Fig. 27. Mandible of male *Gnathia maxillaris* (Isopodan Crustacea).

Fig. 28. Mandible of *Squilla* sp. (Stomatopodan Crustacea).

Fig. 29. Mandible of *Caprella* sp. (Amphipodan Crustacea).

Fig. 30. Mandible of *Calanus* (Copepodan Crustacea), drawn partly from specimen, partly from figure by Borradaile.

Fig. 31. Left (?) "mandible" of *Peripatus* sp., drawn from several sources.

Fig. 32. Distal region of mandible of isopod crustacean, *Cirolana concharum*. The mandibular palpus is cut off.

Fig. 33. Mandible of ostracod crustacean, *Acanthocypris bicuspis*, from figure by Claus.

Fig. 34. Apical region of mandible of ostracod crustacean, *Cypris pubera*, from figure by Claus.

Fig. 35. Mandible of *Leander serratus* (Decapodan Crustacea).

Fig. 36. Body of mandible of *Ligia* sp. (Isopodan Crustacea).

REVISION OF THE GENUS *LIGYROCORIS* STÅL (HEMIPTERA, LYGÆIDÆ).

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ROSELLE PARK, N. J.

The genus *Ligyrocoris* was founded by Stål in 1872¹ with *Cimer silvestris* L., Fieb. named as type. The author's short diagnosis translated reads: "Disk of the second and third ventral segments furnished on both sides behind the acetabulæ with a denuded, densely and very delicately strigose vitta; first segment of the posterior tarsus doubly or in exotics more than doubly longer than the two apical segments together; anterior femora armed beneath anteriorly with two or three larger and several very minute spines; third segment of the rostrum much longer than the fourth."

In 1874² Stål in his treatment of the genus as it pertained to America dropped from his diagnostic characters the relative lengths of the third and fourth segments of the rostrum and of the segments of the posterior tarsus. He arranged six species under the genus, as follows: *L. balteatus* and *multispinus* as new species, *Plociomcrus sylvestris* Lin., *Plociomera litigiosa* Stål, *Lygæus abdominalis* Guér.

¹ Stål, Of. Vet. Akad. Förh., XXIX, 51, 1872.

² Stål, Enum. Hem., IV, 144, 145, 1874.